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# Ecological performance differs between range centre and trailing edge populations of a cold-water kelp: implications for estimating net primary productivity

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## Abstract

Kelp forests are extensive, widely distributed and highly productive. However, despite their importance, reliable estimates of net primary productivity (NPP) are currently unknown for most species and regions. In particular, how performance and subsequent NPP change throughout a species range is lacking. Here, we attempted to resolve this by examining growth and performance of the boreal kelp, *Laminaria digitata*, from range centre and trailing edge regions in the United Kingdom. During the peak growth season (March/April), range-centre individuals were up to three times heavier and accumulated biomass twice as fast as their trailing-edge counterparts. This was not apparent during the reduced growth season (August/September), when populations within both regions had similar biomass profiles. In total, annual NPP estimates were considerably lower for trailing-edge ( $181 \pm 34 \text{ g C m}^{-2} \text{ year}^{-1}$ ) compared to range-centre ( $344 \pm 33 \text{ g C m}^{-2} \text{ year}^{-1}$ ) populations. Our first-order UK estimates of total standing stock and NPP for *L. digitata* suggest this species makes a significant contribution to coastal carbon cycling. Further work determining the ultimate fate of this organic matter is needed to understand the overall contribution of kelp populations to regional and global carbon cycles. Nevertheless, we highlight the need for large-scale sampling across multiple populations and latitudes to accurately evaluate kelp species' contributions to coastal carbon cycling.

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## Introduction

Macroalgae (i.e. kelps and other seaweeds) underpin some of the most extensive and productive coastal ecosystems globally (Mann 1973; Smith 1981; Duarte and Cebrián 1996). Many macroalgal species, including most kelps, exhibit high rates of productivity and rapid biomass turnover, with growth values of up to 2–4% of standing biomass per day (Reed et al. 2008). However, unlike other coastal macrophytes (e.g. seagrasses, mangroves and other halophytes), macroalgae grow attached to hard substrata (rather than within sediments) and as such do not allocate biomass to 'below ground' storage (Duarte 2017). Consequently, the vast majority of biomass accumulation (generally > 80% of production) is released as particulate organic matter, or detritus, which represents an important trophic resource for bacteria, suspension feeders and detritivores, and enhances trophic connectivity in coastal marine ecosystems (Kaehler et al. 2006; Krumhansl and Scheibling 2012). Moreover, emerging evidence suggests a significant proportion of macroalgal detritus may be sequestered in carbon sinks (up to 25%, see Krause-Jensen and Duarte

2016), such as coastal sediments and the deep sea (Chung et al. 2011; Hill et al. 2015; Krause-Jensen and Duarte 2016; Filbee-Dexter et al. 2018; Krause-Jensen et al. 2018; Ortega et al. 2019; Queirós et al. 2019). In light of this, it has been argued that macroalgae should be incorporated into blue carbon assessments (Duarte et al. 2013; Hill et al. 2015; Sondak and Chung 2015; Trevathan-Tackett et al. 2015; Smale et al. 2018; Macreadie et al. 2019). Despite the fundamental role that macroalgae, and kelp species in particular, play in coastal carbon cycling, reliable estimates of carbon fixation (i.e. productivity) are currently lacking for most species and regions (Reed and Brzezinski 2009).

Understanding the role that kelp species play within local and global carbon (C) cycles requires quantification of primary production rates under different environmental conditions and throughout a given species' range, to elucidate regional differences in demographic performance. The "Abundant-Centre Hypothesis" (ACH) (also known as "centre-periphery" or "central-marginal" hypotheses) is a common paradigm in biogeography. The ACH assumes conditions are optimal at the range centre and become increasingly less favourable toward the periphery (Hengeveld and Haeck 1982; Brown 1984), which results in a reduction in genetic diversity, performance and abundance at range margins. However, meta-analyses have revealed that there is often little empirical support for the ACH challenging its generality across species (Sagarin and Gaines 2002; Dallas et al. 2017; Pironon et al. 2017) and to what extent kelp species conform to the ACH is largely unknown. On the one hand, the high degree of local adaptation observed for some marine macrophytes may maintain performance throughout a species range (see King et al. 2018a, b). On the other, stressful abiotic (e.g. temperature) and ecological (e.g. inter-specific competition) conditions and subsequent reduced genetic diversity may impair performance (Eckert et al. 2008; Viejo et al. 2011; Smale and Wernberg 2013; Straub et al. 2019; Wernberg et al. 2018).

The latitudinal distributions of kelp species are strongly constrained by temperature (Eggert 2012) and, as such, they are influenced by contemporary and near-future ocean warming trends (reviewed by Smale 2020). Assuming no local adaptation or plasticity, climate-driven poleward range shifts may result in considerable losses of standing biomass and reduced rates of primary productivity from any given species' trailing edge (Wernberg et al. 2016; Arafeh-Dalmau et al. 2019). Moreover, rising temperatures will likely impact performance throughout the entire species range, with current 'cold' populations likely to function similarly to current 'warm' populations over the coming decades (Pessarrodona et al. 2018). As such, determining how kelp performance varies between populations and across latitudes is a prerequisite to understanding how the capture and flow of carbon

through temperate reef ecosystems systems may change in the future.

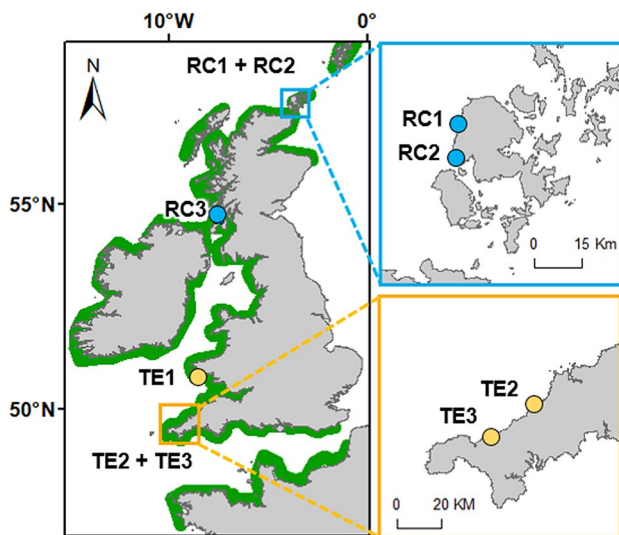
Rocky coastlines in the northeast (NE) Atlantic region are dominated by kelp forests, which are thought to make a substantial contribution to coastal primary production (Jupp and Drew 1974; Kain 1979; Pessarrodona et al. 2018; Pedersen et al. 2020). However, the current state of knowledge on the dynamics of NE Atlantic kelp forests is limited, as they have been chronically understudied compared to some other temperate regions (Smale et al. 2013). *Laminaria digitata* (Hudson) J.V. Lamouroux is a cool boreal kelp with a transatlantic distribution. In the NE Atlantic, it is distributed from the Arctic to the English Channel and is predicted to undergo a poleward range contraction over the coming decades (Raybaud et al. 2013; Assis et al. 2018). Here, we compared the performance of *L. digitata* in two thermally distinct regions in the United Kingdom (UK) representing trailing edge and range centre populations, during periods of maximum and minimum productivity. Our overall aim was to quantify primary productivity rates for *L. digitata* in the UK and to explore more generally to what degree this species conforms to the ACH.

## Methods

### Survey design

Here, we aimed to characterise how *L. digitata*'s performance changes between sites at its range centre (RC) and trailing edge (TE). Sampling across large geographical scales and attributing differences to particular variables is challenging as many local factors can affect performance and obscure regional patterns. To address this, we picked sites that were similar in local environmental factors so that we could attribute changes to either temperature or light that co-vary with latitude.

Following a nested design, we chose three sites at *L. digitata*'s range centre and three at its trailing edge (Fig. 1). Based on neutral markers and common garden temperature stress assays, King et al. (2019) showed there is little gene flow between these regions and trailing edge populations may represent distinct thermal ecotypes. Mean annual sea surface temperatures within the RC region are ~2.3 °C lower than those within the TE region. These regional temperature differences become more apparent in summer where differences between regions are ~3.3 °C (Table 1). To minimise local effects of wave exposure on kelp performance and morphology (Gerard and Mann 1979; Blanchette et al. 2002; Fowler-Walker et al. 2006; Millar et al. 2019) only fully exposed shores were selected. Wave exposure was measured using log wave fetch derived from summing fetch values calculated for 32 angular sectors surrounding each



**Fig. 1** Sampling sites for *Laminaria digitata*. Shaded area indicates approximate distribution of *L. digitata* in UK, Ireland and France. RC range centre, TE trailing edge

study site (see Burrows 2012). Flow rates were greater at trailing edge sites but all still represented low flow sites for *L. digitata* ( $<0.4 \text{ m s}^{-1}$ ; see Millar et al. 2019). Nutrients were not directly measured but UK coastlines are not characterised by major upwelling regimes and nutrients do not vary greatly with latitude (Painting et al. 2013). Moreover, previous studies have shown no significant difference in nutrient concentrations between our study regions (Smale et al., 2016; Pessarrodona et al. 2018).

Growth rates of *L. digitata* exhibit pronounced seasonality, with a period of rapid biomass accumulation occurring from February to June, followed by a period of reduced growth from August to January. This pattern coincides with regeneration of nutrients in spring and their depletion in summer and is triggered by changes in photoperiod (Kain and Jones 1969; Davison and Stewart 1984) and onset of fertility (Buchholz and Lüning 1999). During summer, photosynthetic products are stored as carbohydrates, which are later remobilised as new growth is initiated in the spring (Schaffelke and Lüning 1994). Therefore, surveys were conducted during peak growth, March–April (2015), and reduced growth, August–September (2015), periods to encompass the different phases of biomass accumulation in *L. digitata* (Table S9).

## Measuring individual performance

**Population demographics:** Kelp density was quantified at each site by haphazardly placing eight  $1 \text{ m}^2$  quadrats within the kelp forest and recording the number of mature individuals (defined as dominate space occupiers with

**Table 1** Summary of broad scale environmental predictor variables for each study site

Site	Latitude	Longitude	Site name	Min temp (°C)	Max temp (°C)	Mean Temp (°C)	Exposure Log wave fetch (km)	Log Chl a	Mean summer day length (hr:mm)	Annual sunshine (hr yr <sup>-1</sup> )	Mean flow (m sec <sup>-1</sup> )	Max tidal range
RC1	59.051076	- 3.346552	Bay of Skail	7.11	12.7	9.7	3.902364	0.13	18.07	1197	0.05	3.6
RC2	58.959089	- 3.347741	Warbeth	7.15	12.7	9.7	3.962081	0.16	18.07	1197	0.06	3.6
RC3	56.290522	- 5.645727	Easdale	7.3	13.6	10.4	3.313315	0.52	17.19	1219	0.14	4.7
TE1	51.933549	- 5.209578	Abereiddy	8.1	15.7	11.7	3.847948	0.45	16.20	1625	0.21	7.3
TE2	50.546927	- 4.989629	Trevone	8.87	16.6	12.5	3.97545	0.29	16.08	1519	0.29	5.6
TE3	50.220436	- 5.477339	St Ives	9.37	16.5	12.5	4.089245	0.25	16.08	1519	0.35	5.6

Temperature data were sourced from the NOAAOptIntSSTV2 dataset and averaged from 1982 to 2011. 'Log wave fetch' is a broad-scale metric of wave exposure, derived by summing fetch values calculated for 32 angular sectors surrounding each study site (see Burrows 2012). 'Log Chl a mean' was sourced from the MODIS Aqua dataset and is averaged from 2003 to 2018 (4.5 km resolution). 'Mean summer day length' is the average day length (all days in June and July) at each site. Regional irradiance levels were inferred from average annual sunshine hours (1981–2010) obtained from the nearest weather station to the study sites (Loch of Hundland RC1 & 2, Dunstaffnage RC3, Milford Haven TE1 and St Austell TE2 & 3). Mean tidal current strength was sourced from the TPX08 database and extracted from the constituents M2, S2 and K1. Maximum tidal range was obtained from the nearest station in the UK Tide Gauge Network to the study sites (Wick RC 1 & 2, Tobermory RC3, Milford Haven TE1, Newlyn TE 2 & 3). The network was established in 1953 and sea level data are managed and accessed through the British Oceanographic Data Centre ([www.bodc.ac.uk](http://www.bodc.ac.uk))

a stipe length > 30 cm). Sampling was conducted in the middle of the *L. digitata* zone (~0.5–0.8 m above chart datum) during periods of low tide emersion. Due to logistical challenges, it was only possible to obtain density data during sampling in the peak growth season. However, *L. digitata* is a perennial species, persisting for up to ~6 years, and seasonal surveys conducted on other UK populations have shown that densities are relatively stable throughout the year (Hereward et al. 2018). Morphological and biomass estimates were taken for ~20 individuals at each site. Note: these are the same individuals used for growth estimates (see below). The age of individual plants was not determined.

**Blade elongation and biomass accumulation:** Like most Laminariales, *L. digitata* exhibits a ‘conveyor belt’ growth strategy, with new tissue formed by the meristematic area at the base of the blade and older material translocating towards the distal tips of the blade. Therefore, elongation rate, estimated by punching of a hole and measuring its distance travelled, has been used as a reliable measure of relative growth rates (Parke 1948). An adaptation of this method allows the quantification of the actual biomass laid down by taking into account morphology (Mann and Kirkman 1981; Krumhansl and Scheibling 2011). At each sampling period, 20 individuals were randomly selected from within the *L. digitata* stand. Two holes were punched into the central digit of the blade of each individual, at 5 and 10 cm from the junction between the stipe and the meristem. After 4–6 weeks, individuals were relocated and returned to the laboratory for analysis. Lamina extension was calculated as the sum of the distance between each hole and the stipe/meristem junction at the end of the growth period, minus the initial distance of the holes from the base of the blade.

To convert elongation rates (cm) to daily biomass accumulation (g), three 5 cm wide (running perpendicular to the kelp blade) basal segments were cut from above the meristem (Fig. S1).

The relationship between weight and position along the blade is constant around a maximum value past an initial area of regrowth where weight increases with distance from the meristem. To ensure we did not underestimate performance we used the heaviest segment (basal segment 3 in all cases) to calculate individual daily biomass accumulation (g FW day<sup>-1</sup>) using Eq. (1):

$$B = e \times \frac{W}{5} / t \quad (1)$$

where  $e$  is lamina extension (cm),  $W$  is fresh weight of the heaviest basal segment (divided by 5 to give g cm<sup>-1</sup> of lamina) and  $t$  is the number of days between initial hole-punching and kelp collection.

## Converting to site level productivity

To attain site level estimates of primary productivity from individual biomass accumulation rates we used conversion factors to firstly convert FW to dry weight (DW) and then to carbon (C) biomass. FW:DW was not measured at our study sites and so conversions were obtained from monthly sampling of independent populations of *L. digitata* from two sites in Plymouth Sound, SW England (West Hoe, 50.363045, – 4.139226; Mount Batten, 50.356469, – 4.127217) (Table S9). Monthly FW:DW relationships were determined by drying the heaviest basal segment for biomass accumulation at 60 °C for 48 h. For tissue carbon, 5 basal segments were randomly selected from individuals used for growth estimates. These were frozen (– 20 °C), subsequently dried and then ground to a fine powder and C content quantified with a standard elemental analyser (CHN Analyser, EA1110, EE Instruments Ltd, Wigan).

Site level standing stock of carbon (g C m<sup>-2</sup>) was quantified using Eq. (2):

$$SS = (w \times d) \times x \times c \quad (2)$$

where SS is the standing stock,  $w$  is the mean individual plant weight (g FW),  $d$  is the mean population density (m<sup>-2</sup>) of canopy forming individuals (stipe length > 30 cm),  $x$  is the FW:DW conversion factor (based on reference sites in Plymouth Sound) and  $c$  is the C content conversion factor (site level estimate).

For each sampling period, we then calculated site level net daily primary productivity (g C m<sup>-2</sup> day<sup>-1</sup>) using Eq. (3):

$$sNPP = (B \times d) \times x \times c \quad (3)$$

where sNPP is the site Net Primary Productivity,  $B$  is the mean daily biomass accumulation,  $d$  is the mean population density,  $x$  is the FW:DW conversion factor (based on reference sites in Plymouth Sound) and  $c$  is the C content conversion factor (site level estimate).

To extrapolate from our two sampling periods to annual rates of productivity we needed to determine the relative contributions of our observation periods to the total annual growth cycle. *L. digitata*’s annual growth cycle was characterised at the two reference sites in Plymouth Sound and assumed to represent *L. digitata*’s growth cycle throughout our study area. At the two reference sites, productivity was measured monthly (using the same technique described above) and each month’s contribution to total productivity calculated (Table S9). The percentage contribution of April (Peak) and August (Reduced) to annual productivity (g C m<sup>-2</sup> year<sup>-1</sup>) was used to determine annual using Eq. (4):

$$aNPP = \left( B \times \left( \frac{M}{P} \right) \right) \times 100 \quad (4)$$



where aNPP is the annual net primary productivity,  $B$  is the mean daily biomass accumulation,  $M$  is the standard month (30.5 days) and  $P$  is the percentage contribution of sampling month to overall annual productivity (determined from reference sites in Plymouth Sound; Table S9). aNPP was calculated independently using measurements from both the peak (April) and the reduced (August) growth periods and annual estimates are a mean of the two values (Table S11). Finally, we generated first-order estimates of the total areal standing stock of  $C$  and NPP for *L. digitata* stands in the UK. The spatial extent of suitable habitat was determined by summing the length of coastline in the UK dominated by rock or cobble habitat that is semi-to-fully exposed to wave action (Burrows et al. 2008), which represents favourable conditions for *L. digitata* (Burrows 2012). Based on surveys and observations, *L. digitata* was assumed to inhabit a ~20 m wide band along the low intertidal/subtidal fringe (depth range ~0–0.7 m above chart datum) of this section of coastline. To gain UK wide estimates of aNPP and total areal standing stock, *L. digitata*'s spatial extent ( $\text{km}^2$ ) was multiplied by the study wide mean estimates of site level standing stock ( $\text{g C m}^{-2}$ ) and aNPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ ).

### Statistical analysis

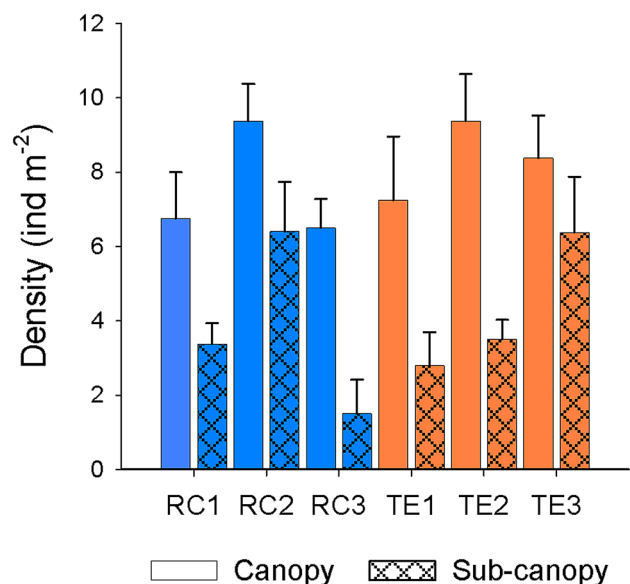
Variability in individual kelp (length, blade weight, elongation, weight of heaviest basal segment, biomass accumulation and tissue carbon) and site level (abundance, standing stock) metrics were determined using univariate Permutational Analysis of Variance (PERMANOVA), using the PERMANOVA module (Anderson 2001) within Primer 6 software (Clarke and Gorley 2001). A similarity matrix was generated for each metric based on Euclidean distance and variability tested with 9999 permutations untransformed data under a reduced model.

For length, weight, elongation, weight of heaviest basal segment, biomass accumulation and tissue carbon, model factors consisted of Region (fixed factor; 2 levels: Range Centre, Trailing Edge), Site (random factor, 3 levels nested within Region) and Season (fixed factor; 2 levels: Peak and Reduced). For density, the model consisted of Region (fixed factor; 2 levels: Range Centre, Trailing Edge) and Site nested within region. For standing stock, replication was at the site level so the model consisted of Region (fixed factor; 2 levels: Range Centre, Trailing Edge) and Season (fixed factor, 2 levels: Peak, Reduced). Differences in mean annual estimates of primary productivity between regions was determined using a  $t$  test. All values are presented as means + standard error (SE).

### Results

The mean density of canopy forming individuals per site ranged from  $6.5 (\pm 1.5 \text{ SE}) \text{ ind. m}^{-2}$  to  $9.4 (\pm 3.5 \text{ SE}) \text{ ind. m}^{-2}$  and did not differ between sites (nested within regions) or between regions (Table S1; Fig. 2). All individual metrics (i.e. length, fresh weight biomass, elongation, weight of heaviest basal segment and biomass accumulation) exhibited significant Season  $\times$  Site(Region) interactions. This means there was significant variability between sites from the same region but only in one season. In all cases, this was driven by greater variability in the peak growth season. For example, in the range centre region, average blade length between sites varied from  $142.4 (\pm 10.4 \text{ SE}) \text{ cm}$  (RC3) to  $223.5 \pm 13.5 \text{ cm}$  (RC2) (range 81.1 cm), whereas in the reduced growth season length varied from  $96.4 (\pm 3.97 \text{ SE}) \text{ cm}$  (RC3) compared to  $111.8 \pm (6.95 \text{ SE}) \text{ cm}$  (RC1) (range 15.4 cm). Similarly, fresh weight biomass varied from  $573.2 (\pm 44.8 \text{ SE}) \text{ g}$  (RC2) to  $999.5 \pm (106.5 \text{ SE}) \text{ g}$  (RC3) (range 426 g), whereas in the reduced season weight profiles varied from  $267.1 \pm (62.6 \text{ SE}) \text{ g}$  (RC2) to  $398.3 (\pm 61.1 \text{ SE}) \text{ g}$  (RC3) (range 131.2).

Overall, for blade length, we found no effect of region but lengths differed between seasons. In the peak growth season, blade length was  $166.2 \pm (4.8 \text{ SE}) \text{ cm}$  compared to  $107.9 (\pm 2.8 \text{ SE}) \text{ cm}$  in the reduced growth season (Table S2). For fresh weight biomass, we detected an interaction between Region and Season (Table S3). Whilst there was considerable within region variability

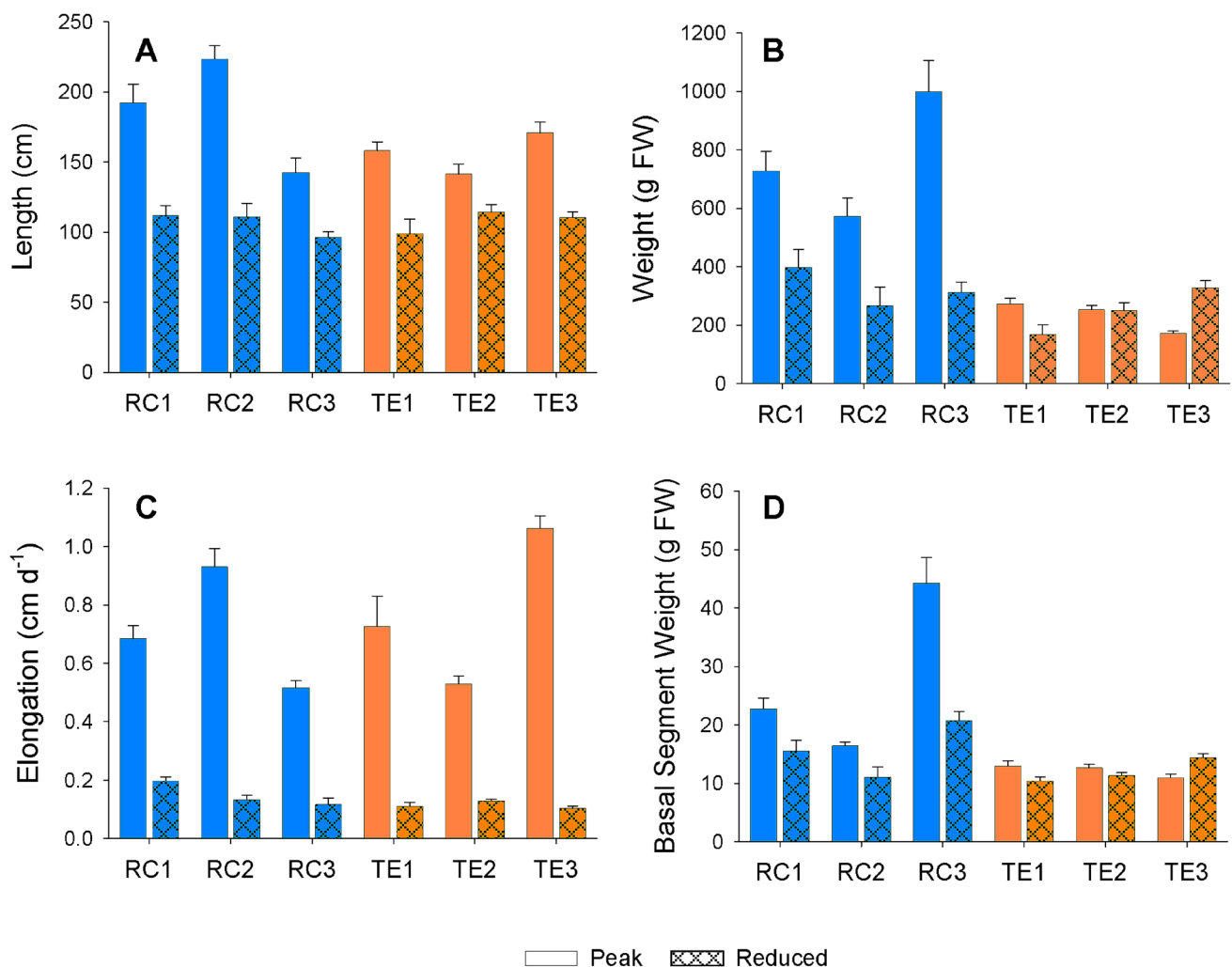


**Fig. 2** Mean ( $\pm$ SE) density of canopy (>30 cm stipe length) and sub-canopy (<30 cm stipe length) *L. digitata* across study sites.  $n=8$  quadrats per site

in the peak growth season, all values at range centre sites were greater than trailing edge sites, indicating clear directional generality. In the peak growth season, individual fresh weight biomass in the range centre region was 810.9 ( $\pm 58.8$  SE) g compared to 235.5 ( $\pm 10.9$  SE) g in the trailing edge region. These regional differences were not apparent during the reduced growth season where individual fresh weight biomass was similar between regions at 336.6 ( $\pm 33.3$  SE) g in the range centre region and 251.5 ( $\pm 18.9$  SE) g in the trailing edge region. Daily elongation rates varied markedly between sites but were comparable across regions, and exhibited pronounced seasonal variability (Table S4; Fig. 3c). During the peak growth season, mean daily blade elongation was 0.71 ( $\pm 0.08$  SE) cm but fell to 0.13 ( $\pm 0.02$  SE) cm during the reduced growth period. The weight of the heaviest basal segment also varied considerably between sites (Fig. 3d). In particular, RC3

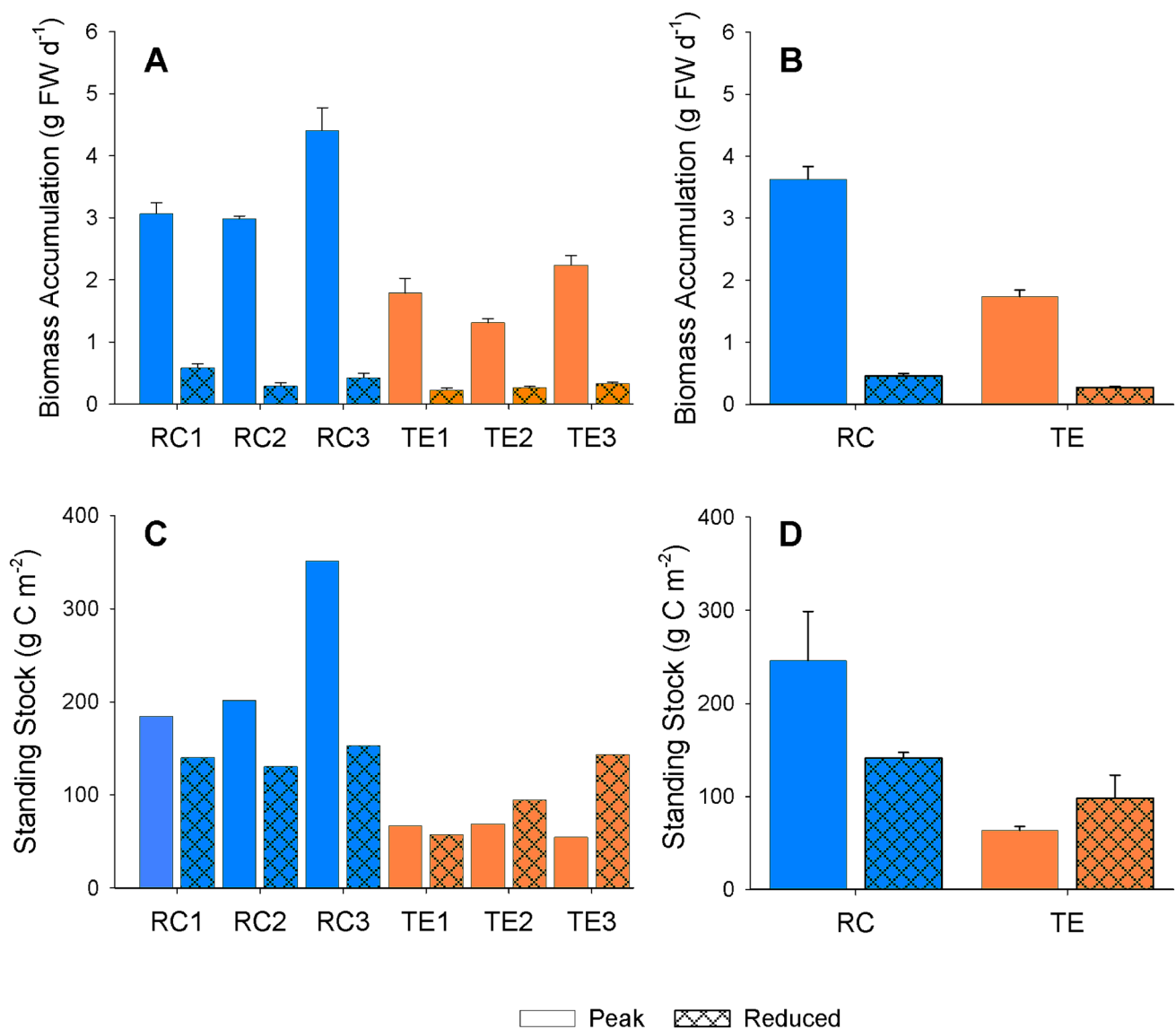
was over twice as heavy as other sites within the same region, during the peak growth season. The weight of the heaviest basal segment differed between regions but there was no main effect of season (Table S5). The weight of the heaviest basal segment was 23.9 ( $\pm 1.8$  SE) g FW in the range centre region compared to 12.1 ( $\pm 0.3$  SE) g FW in the trailing edge region.

For fresh weight biomass accumulation, we detected an interaction between Region and Season. Whilst there was considerable within region variability, there was clear directional generality with range centre sites larger than trailing edge sites (Table S6; Fig. 4a). During the peak growth season, mean biomass accumulation was 3.6 ( $\pm 0.2$  SE) g FW day<sup>-1</sup> in the range centre region compared to 1.7 ( $\pm 0.1$  SE) g FW day<sup>-1</sup> in the trailing edge region (Fig. 4b). In the reduced growth season, biomass accumulation was similar between regions at 0.45 ( $\pm 0.04$  SE) g FW day<sup>-1</sup>



**Fig. 3** Mean (+SE) population demographics of canopy forming *Laminaria digitata* (stipe length > 30 cm) across study sites and growth season. **a** Total blade length, **b** Total blade weight, **c** Blade

elongation rate and **d** Weight of heaviest basal segment. While 20 individuals were tagged, the number of individuals harvested for sampling varied between 9 and 17 (Table S10)



**Fig. 4** Site (a+c) and region (b+d) level estimates of biomass accumulation (a+b) and carbon standing stock (c+d) for *L. digitata* in its peak (non-hatched bars) and reduced (hatched bars) growth season.

c Represents individual site values from Eq. (2) and as such has no error. All other values are mean  $\pm$  SE

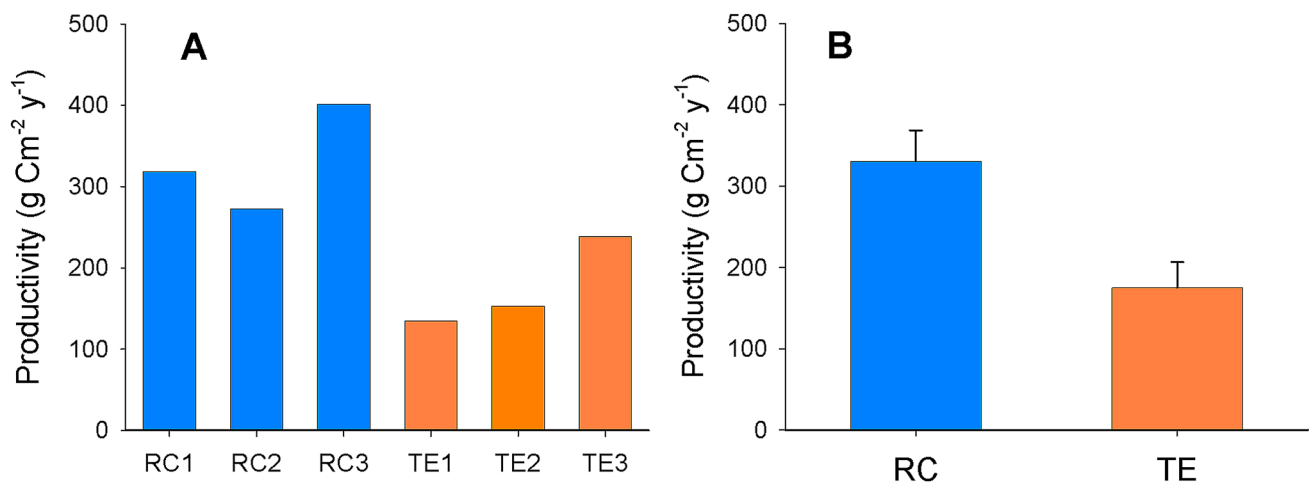
in the range centre and  $0.28 (\pm 0.01 \text{ SE}) \text{ g FW day}^{-1}$  in the trailing edge (Fig. 4b).

For % tissue carbon, we found no effect of region but there was a seasonal effect. In the peak growth season, tissue carbon was  $30.2 (\pm 0.19 \text{ SE}) \%$  compared to  $33.7 (\pm 0.31 \text{ SE}) \%$  in the reduced growth season (Table S6). Standing stock of C exhibited a significant Region  $\times$  Season interaction (Table S8; Fig. 4c and d). In the peak growth season, C standing stock in the range centre region was  $278 (\pm 59 \text{ SE}) \text{ g C m}^{-2}$  compared to  $79 (\pm 11 \text{ SE}) \text{ g C m}^{-2}$  in the trailing edge region. During the reduced growth season, average C stocks were similar between regions at

$166.9 (\pm 4.6 \text{ SE}) \text{ g C m}^{-2}$  in the range centre region and  $113.1 (\pm 29.4 \text{ SE}) \text{ g C m}^{-2}$  at the trailing edge (Fig. 4d).

Our site-level estimates of annual NPP varied markedly between sites, ranging from 135 to  $402 \text{ g C m}^{-2} \text{ year}^{-1}$  (Fig. 5a). Overall, annual NPP rates were significantly greater in the range centre region, at  $344 (\pm 33 \text{ SE}) \text{ g C m}^{-2} \text{ year}^{-1}$  compared to the trailing edge region, at  $181 (\pm 34 \text{ SE}) \text{ g C m}^{-2} \text{ year}^{-1}$  ( $t = 2.65$ ,  $p = 0.05$ ) (Fig. 5b). We calculated that across the UK, approximately 4270 km of coastline met the criteria of being both dominated by hard substrata and semi-to-fully exposed to wave action. Based on *L. digitata* existing within a 20 m vertical band





**Fig. 5** Site (a) and region (b) level estimates of annual net primary productivity for *L. digitata*. **a** Represents individual site values from Eq. (4), and as such, has no error. **b** Represents mean  $\pm$  SE

along these shorelines, this translates to an estimated areal extent of 85 km<sup>2</sup>.

Based on study-wide mean values for standing stock and annual NPP of 159 g C m<sup>-2</sup> and 262 g C m<sup>-2</sup> year<sup>-1</sup>, respectively, we estimate that *L. digitata* populations in the UK hold at least 13,515 t C and turnover 22,270 t C each year.

## Discussion

Understanding the role that macroalgae play in carbon cycling has gained increased attention in recent years, yet robust estimates of primary productivity and carbon fluxes in marine environments have been hindered by a lack of reliable data, particularly across large spatial scales. For *L. digitata*, our study wide estimates of standing stock ranged from 62 to 397 g C m<sup>-2</sup> with a mean of 159 g C m<sup>-2</sup>, which is comparable to estimates for *L. digitata* in both France (162 g C m<sup>-2</sup>, Gevaert et al. 2008) and Nova Scotia (120 to 420 g C m<sup>-2</sup>, Krumhansl and Scheibling 2011). However, this is considerably lower than standing stock estimates for many other kelp populations, including the subtidal congeneric species, *Laminaria hyperborea*, in the NE Atlantic (e.g. 721 g C m<sup>-2</sup>, Smale et al. 2016; 770 g C m<sup>-2</sup>, Pedersen et al. 2020). This is likely driven by differences in stipe morphology with *L. hyperborea* possessing a much larger, heavier and more rigid stipe compared to *L. digitata*. Annual estimates of NPP ranged from 135 to 402 g C m<sup>-2</sup> year<sup>-1</sup>, with a mean of 262 g C m<sup>-2</sup> year<sup>-1</sup>, which is again markedly lower than estimates for *L. hyperborea* in the NE Atlantic (Kain, 1971; Sheppard et al. 1978; Pedersen et al. 2020) and for many other macroalgal stands globally (Krause-Jensen and Duarte, 2016). In temperate regions of the NE Atlantic, *L. digitata* is restricted to a narrow band within low intertidal/

shallow subtidal habitats, as it is competitively inferior to *L. hyperborea* in most subtidal environments (Hawkins and Harkin, 1985). Even so, *L. digitata* is widespread and often abundant on rocky shores in the British Isles (Yesson et al. 2015) and along the wider northwest European coastline (Raybaud et al. 2013), it can penetrate into deeper waters in polar regions (Hop et al. 2012) and is likely to be an important contributor to benthic primary production.

Whilst the abundance of *L. digitata* was fairly consistent across our study sites, ecological performance (in terms of growth and productivity) varied between our northern range centre and southern trailing edge populations. During the peak growth season, biomass accumulation was lower at trailing edge sites and individuals had up to three times less biomass, suggesting conditions in this region are less favourable for growth. Laboratory experiments have shown *L. digitata* can grow over a broad range of temperatures with optimum growth occurring between 10 and 15 °C (Bolton and Lüning 1982; tom Dieck 1992). Temperatures experienced in both regions during the springtime period of peak-growth fall within this optimal temperature range, whereas during the summertime period of reduced-growth both water and air temperatures experienced at trailing edge sites can induce considerable stress (Hargrave et al. 2017; Hereward et al. 2020). The trailing edge region also receives more sunshine hours than the range centre, and as such, likely receives higher amounts of harmful UV radiation, causing additional stress (Bischof et al. 2006). This means resources at the trailing edge may be allocated towards maintenance and repair at the cost of growth. On top of this stress gradient, mean summer day lengths are approximately 2 h longer at the range centre. This is important as long days in summer are used to store sugars to be mobilised the following spring when new growth is initiated (see Rinde and Sjøtun,

2005 and references therein). It seems despite evidence for local adaptation to greater temperature stress for *L. digitata*'s trailing edge populations (King et al. 2019), performance is aligned with the Abundant Centre Hypothesis, likely through a combination of stressful temperatures and less time for photosynthesis in summer. However, as growth patterns in *L. digitata* are entrained by photoperiod (Gomez and Luning 2001) and photoperiod differs between range centre and trailing edge regions, our observed regional differences in productivity may also, in part, be due to regional differences in *L. digitata*'s circannual rhythmicity. Future studies fully characterizing annual growth patterns between regions coupled with in situ measures of stress will be able to fully resolve this. It is important to note that regional differences in performance were not related to rates of elongation or total blade length but rather transient morphologies observed during the peak growth season. In general, total blade biomass and maximum weight of basal segments was greater at range centre compared with trailing edge sites, particularly during the peak growth season. Whilst elevated flow rates can increase productivity and overall biomass in *L. digitata* (e.g. Millar et al. 2019), it is unlikely flow is responsible for our observed differences in regional performance as patterns run counter to our results i.e. despite lower flow rates, range centre individuals are larger and more productive. Moreover, the transient nature of our suggested morphological differences between regions is not conducive to persistent regional differences in hydrodynamic regime. As growth can occur laterally in *Laminaria* spp (e.g. Calvin and Ellis 1981), regional differences in performance in the peak growth season may be driven by regional differences in lateral growth and subsequent width at this time. We did not explicitly measure width, and examples of temperature mediated lateral growth are lacking in *L. digitata*. However, elevated lateral growth has been observed at cooler parts of a kelps range (Mabin et al. 2013), at cooler depths (Boden 1979) and in cooler common garden mesocosm treatments (Okada et al. 1985 as cited in Bartsch et al. 2008) and, based on our qualitative observations, may explain some of the regional variability reported here. Differences in maximum weight of basal segments were likely related to blade width, thickness and mass by unit area. Northern range centre populations may have also formed thicker blades, with greater concentration of storage compounds, pigments and other products, under more favourable conditions.

Our results have clear implications for understanding coastal carbon cycling in the face of climate change, particularly ocean warming. So far, the majority of climate change research on kelp species has focussed on either predicting (e.g. Müller et al. 2009; Raybaud et al. 2013; Franco et al. 2018; Assis et al. 2018; Khan et al. 2018) or documenting species' range shifts (Wernberg et al. 2011; Smale et al. 2015), including population losses at trailing

edges (e.g. Wernberg et al. 2016; Arafeh-Dalmau et al. 2019). In contrast, far less is known about how ocean warming may alter ecological performance and carbon dynamics within any given species range (but see Pessarrodona et al. 2018). We documented marked variability in primary productivity rates across a  $\sim 2.5$  °C average sea temperature gradient. Similar trends have been observed for kelp population structure (Smale et al. 2016), kelp forest composition (Smale and Moore 2017), detrital production rates (Pessarrodona et al. 2018) and primary productivity (Smale et al. in review) in subtidal habitats along the same temperature gradient. Given this temperature gradient is comparable to the magnitude of ocean warming predicted for the NE Atlantic by 2100 (Philipart et al. 2011), tentative predictions of changes in the coming decades can be drawn. While future temperatures may remain within *L. digitata*'s growth optimum in the peak growth season, increased stress during summer may reduce overall productivity to levels currently seen at trailing edge sites. Moreover, should *L. digitata* undergo a range contraction at the trailing edge, as has been predicted (Raybaud et al. 2013), both standing stock and benthic NPP would decline dramatically within our warmer trailing edge region. Ocean warming has had, and will continue to have, major impacts on kelp populations and the ecosystems they underpin in many regions around the world (Smale et al. 2020). Our results suggest that their role within coastal carbon cycles will also be affected in coming decades.

In conclusion, we quantified standing stock and NPP of *L. digitata* stands at its range centre and trailing edge sites in the UK, and identified clear differences in demography and ecological performance between thermally distinct regions. Understanding variability in primary productivity between populations and regions is necessary to better predict current and future responses to environmental change, particularly ocean warming. More generally, our estimate of spatial extent suggests that *L. digitata* stands occupy  $\sim 85$  km<sup>2</sup> (i.e. 8500 ha) of coastal habitat, which is  $\sim 6$  times that of maerl beds (Burrows et al. 2014),  $\sim 1$  times that of seagrass meadows (Green et al. 2018) and  $\sim 1/5$  that of salt marsh (Beaumont et al. 2014) coverage in the UK. Given that these stands store and release significant amounts of particulate C (i.e. 13,515 t C and 22,270 t C year<sup>-1</sup> respectively), it is important to advance understanding of the pathways and ultimate fate of this material, to fully appreciate the role these habitats play in C cycling and as potential blue carbon donors. If even only a fraction of this material reaches and resides within carbon storage habitats, as has been suggested (Krause-Jensen and Duarte 2016; Pessarrodona et al. 2018; Ortega et al. 2019), then the process of C donation has elevated importance and the implications of climate change-carbon cycling feedbacks may be considerable.

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**Availability of data** Data available at <https://figshare.com/s/8f0bd6355575f0f40091>.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

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